

The south-western Australian flora in autumn: 2001 Presidential Address

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Abstract

In the flora of south-western Australia, vegetative colour change in summer and autumn followed by regreening after rain is much more widespread than previously reported, though patchy in occurrence and variable within species. The term *diallagy* (adj. *diallagous*) is proposed to describe the strategy of reversible change between the green and coloured states. It is here recorded for 99 species in 59 genera of 24 families of flowering plants, both monocots and dicots. These species occur in a number of widely distributed habitats. In some species, extent of colour change increases as long as the dry weather continues. The change generally is reversed after 10-15 mm or more of rain falls over a short period (24 hours). Regreening takes from several days to several weeks. The mechanisms operating within the plants are yet to be investigated, but possibilities are discussed to point the way to further research; some are likely to be similar to that reported for *Borya*. In an extreme dry summer such as that of 2000-2001, death occurs in some species.

Paradoxically, other species flower at this season, in some cases close to diallagous species. It is suggested that these have retained a summer/autumn flowering period (from a tropical origin) to take advantage of pollinators at a season when few sources of nectar and pollen are available.

Keywords: summer/autumn drought, foliage colour change, diallagy, autumn flowering, monocots, dicots

Introduction

When we think of autumn colour we usually picture Northern Hemisphere trees in brilliant shades of yellow or red, followed by bare branches and perhaps snow on the ground. We don't associate autumn colours with the Australian bush. There is, as far as I am aware, just one cold-temperate Australian deciduous woody plant, the Tanglewood of Tasmania, *Nothofagus gunnii*. In northern Australia there are a number of winter-deciduous trees and shrubs, such as the Kapok Bush (*Cochlospermum* spp), Kapok Tree (*Bombax ceiba*), kurrajongs (*Brachychiton* spp), some *Terminalia*, Large-leaved Cabbage Gum (*Eucalyptus grandifolia*) and Boab (*Adansonia gregorii*). Oddly, some tropical species display autumn colours, such as the Boab. Strangest, perhaps, given its habitat, is the Cedar Mangrove (*Xylocarpus australasicus*) which, even with its roots in water, can turn colour and shed its leaves during the dry season. A number of these species flower when leafless, e.g. *Cochlospermum*, *Brachychiton* and *Bombax*. In this paper I show that, in the south-western Australian flora, we do have widespread autumn colour, albeit occurring intermittently and functioning differently from that of Northern Hemisphere deciduous trees and shrubs. Paradoxically, at the same season when soil moisture is at its lowest and temperatures are still high, other native plants are in full flower or even actively growing.

In south-western Australia, few people venture into the field during the autumn season. It is usually the end of a long, hot, dry summer, and there is still a widely-held view that little is happening in the bush at that time;

spring is the wildflower season, though some flowering continues into summer. Consequently little has been written about the bush in autumn, or about the effect of drought. The words rarely appear in any paper or chapter title of works on the south-western flora, nor do they appear as index entries. Two exceptions are papers by Beard (1968) on drought in the Gibson Desert, and Hnatiuk & Hopkins (1980) on drought in the kwongan near Eneabba. Apart from work on *Borya* (Gaff 1981), only passing mention has been made of foliage colour change in the flora (e.g. Main 1967 pp 9, 11, 22, 33, 145; George 1984a p viii; Wilson 1997 p 278). Main (1967 p 145) did, however, refer to colour change of foliage and bark as indicators of autumn.

This paper is more in the line of natural history than science, being largely a compilation of observations made over many years and particularly in the autumn of 2001, but the Royal Society of Western Australia has its origins in that field so I may be forgiven a little indulgence. I believe that there is a great deal to learn about the summer-autumn drought in south-western Australia and its role in the biology of our biota and how they have evolved. From such initial observations, researchers often find topics for more in-depth studies.

I am concerned here with perennial 'evergreen' plants. Those in the south-western flora that survive or avoid dry periods by dying back to an underground storage organ (bulb, rhizome, tuber) have been well described by Pate & Dixon (1981) and aestivating mechanisms in herbaceous stilt plants have been described by Pate *et al.* (1984). Nor shall I speak about annual or ephemeral plants that survive dry periods as seeds. Such plants are

rather better documented than the others and their strategy is more readily understood. And I shall not deal with ferns, many of which are well-known drought avoiders by reducing water content but not changing chlorophyll, the fronds typically curling tightly to help avoid dessication.

Coloured (non-green) foliage is well-known in the flora in both new and senescing growth. New shoots of many species are characteristically various shades of red, some species of Proteaceae, for example, being quite spectacular. Colours such as yellow, brown and red are normal in some species as leaves senesce and die. During the recent summer and autumn, dying plants of several species turned an orange-brown as they died, *e.g.* *Nemcia reticulata* at Seabird north of Perth, *Dryandra sessilis* (both var *sessilis*, *e.g.* at Crystal Brook on the Darling Scarp, and var *cygnorum*, *e.g.* at Seabird) [see below for location of observation sites].

Previous work

The most significant work specifically on autumn dormancy in Australia is that of Don Gaff of Monash University (Gaff 1981 and references cited therein). Investigating 'resurrection plants', Gaff found the Western Australian *Borya nitida sensu lato* to be a prime example. Resurrection plants are also termed poikilohydrous, *i.e.* their water content follows closely fluctuations in the moisture of their environment. They have the capacity to reduce their water content and their metabolism to an extremely low level and remain thus for long periods until moisture increases, whereupon they revive and continue normal activity.

In *Borya*, the leaves turn yellow or orange as soil moisture declines with the onset of summer and the change in the cell structure is quite remarkable (Gaff 1981). In viable, yellow leaves, the chloroplasts, chlorophyll structure and cytoplasm appear to become disorganised, the vacuole frequently being fragmented or lobed, and the nucleus is the only organelle discernible. Chloroplasts lack grana and have few thylakoids. There are extensive gaps in the membranes bounding the plastid, and in extreme cases plastids may be recognised only because of their plastoglobuli. 'The disorganization of fine structure is not complete, an essential core of structure is retained as a base for reconstruction of the full cell system on reimplantation.' During drying, soluble protein increases but insoluble nitrogen decreases. A close, but not indivisible, association exists between tolerance induction and yellowing. Gaff noted that leaf senescence invariably negates the ability to tolerate desiccation. He also found that leaves of *Borya* collected dry in the field had recovered on rewetting after five years in storage.

Gaff's (1981) work covered several 'forms of *Borya nitida*' which now, following the revisionary work of Churchill (1985, 1987), can be referred to as species. Gaff's Mt Lindesay form is *Borya longiscapa*; his Shannon Mill form is a southern variant of *B. splaerocephala*; his Kelmscott-Brookton form is typical *B. splaerocephala*; and his Karalee form is *B. constricta*.

Gaff (1981) discussed the problem of seeking resurrection plants and reasoned that, in Australia, the

south-western winter-rainfall zone should be a suitable region, where 'shallow soil pans on rock outcrops, particularly granite ones, usually provide the best opportunity for collecting plants in air-dry condition'. He wrote that they may be best recognised in the field, especially from a change in the colour of the foliage, for example 'an intense purple-black colouration of viable air-dry leaves in some species, *e.g.* *Tripogon liliiformis*, by a 'healthier' golden-straw colour in the viable leaf bases of grasses and sedges, and by retention of chlorophyll in ferns that have air-dried *in the field*' (Gaff's italics).

Gaff (1981) wrote that 'resurrection plants do not occur randomly throughout the plant taxa, but tend to be confined to relatively few families, some closely related, others distantly related. Within these families, the species tend to occur either in one genus or in a group of related genera.' He recorded some 16 species in Australia: one dicot (*Boea*, Gesneriaceae) and 15 monocots of 7 genera in 3 families (Poaceae, 'Liliaceae' [his records now in Boryaceae] and Cyperaceae). He predicted that certain other genera (all monocots) might include resurrection species since they did in other countries. He noted that some Stylidiaceae and *Drosera* might show this behaviour. He also recorded 15 species of fern and fern ally, representing 7 genera in 5 families, as resurrection plants in Australia.

Research in Darwin (Montagu & Woo 1999) has shown that, during the dry season, the wattle *Acacia auriculiformis* can reduce the chlorophyll and soluble protein content of its phyllodes by 73% and 52% respectively. After rain they recovered to almost the previous wet-season values. Some phyllodes were shed during the dry season but new growth did not begin until more than 11 weeks after rain fell, indicating that initial revival of activity depended on the surviving phyllodes.

Research by John Pate and colleagues at The University of Western Australia is also pertinent to this study. Although much of it has not been specifically directed at how plants survive the long summer, their findings reveal the mechanisms that may be operating. The following factors appear significant.

Many species have both shallow and deep (sinker) roots, the former taking up water from the upper soil layers during rainy spells, when nutrients are accumulated and stored, the latter increasingly from the watertable as the dry season approaches. Some plants such as *Banksia prionotes* continue growth and even flower during the dry season, using nutrients acquired during the winter and drawing soil moisture from deep in the profile (*e.g.* Pate *et al.* 1998).

All Proteaceae except *Persoonia* and some species in other families, especially in dry habitats, develop cluster or proteoid roots in autumn (Lamont 1984). These are specialised feeding roots that may assist plants to respond rapidly to rain events (Pate & Meney 1999).

Restionaceae have roots that penetrate no deeper than 2 metres, and in some *Alexgeorgea* spp no more than 50 cm (Meney & Pate 1999). Thus they are not reaching the watertable during summer.

Vesicular mycorrhizal fungi have been recorded in the roots of species of Restionaceae and Cyperaceae. They form a symbiosis with the host plants in autumn and

early winter and may respond very rapidly to moisture at the end of summer, assisting the host to take up nutrients quickly (Meney *et al.* 1993; Pate & Meney 1999). Ectomycorrhizal fungi have been reported in several woody genera, especially in Epacridaceae, *Eucalyptus*, *Casuarina*, *Melaleuca*, *Leptospermum*, *Dillwynia* and *Gastrolobium* (Bowen 1981; Lamont 1984). They, too, may respond rapidly to increased moisture and so enable the host plant to react more quickly than one without such an association.

Hnatiuk & Hopkins (1980) described drought effects in kwongan south of Eneabba after two years of below-average rainfall. They recorded the response to water stress of 124 species but, because their observations were made in spring, change in foliage colour was not noted. Deaths occurred in 86 species. Seedlings were found of 49 of these, and 59 species with dead aerial parts resprouted from underground parts. For 31 species with dead individuals no regeneration was observed. The families most affected were Proteaceae and Epacridaceae. They noted a patchiness in the occurrence of water stress but believed that this was not due to topography, soil type or vegetation type.

A study of water stress due to drought in southern Queensland, New South Wales and Victoria recorded widespread wilting of native trees and shrinkage of bark, sometimes leading to death (Pook *et al.* 1966). Foliage of some eucalypts became dull, then yellowish and died. Variation was attributed to soil type and aspect of the site.

Methods

In south-western Australia the summer and autumn of 2000-2001 gave an extraordinary opportunity to observe the effects of drought on the flora. Through much of the South-West, roughly south and west of a line from Geraldton to Esperance, there was little effective rain from the end of September until late April or early May. Perth recorded its driest such period on record with 48.8 mm compared with the average of 144.5 mm. Of that 48.8 mm, 23.6 mm fell in November, and only 20.0 mm from then over the five months until 30 April. The first effective fall for 2001 (17.8 mm) occurred on 6 May. When describing floods, the terms '10-year' and '100-year' events are sometimes used for above-normal and extreme events that occur, on average, at those intervals. I suggest that the same might be applied to droughts, and that the summer of 2000-2001 was a 100-year event. In some localities its effect on the native vegetation was striking, and will be noticeable for some years.

From March to August 2001 I visited 20 sites to record any species whose foliage showed a change in colour. I visited most twice, before and after the first effective rain (10 mm or more within a 24 hour period). Some near Perth I visited more often. For each locality, a brief description is given below of the landform, soil and vegetation, dates visited, and first effective rain event for 2001. Rainfall is taken from the nearest official recording station (Table 1). As far as I can judge, similar rainfall occurred at my sites, except Charles Gardner Reserve where it was much less than that received in the town of Tammin some 17 kilometres to the north. I also include

here some observations made in previous years at other localities. Geographically these range from near Eneabba to Perth, inland to Tammin and south-east to Corrigin. For most of these earlier observations no follow-up visits were made to assess regreening, although from my general field observations the leaves of the species recorded are normally green.

Species were identified, foliage colour described in simple terms, notes made on any change in position and texture, and colour slides taken using Fujichrome 100 film. Variation within and between populations was also noted.

My observations indicate that, in south-western Australia, plants presumed able to reduce their metabolic activity by internal processes shown by colour change are much more common than previously reported in terms of their taxonomic spread, geographical distribution, habitat, and appearance. Whether any of those newly reported here are true resurrection plants remains to be determined.

It must be emphasised that these observations are mostly from sites where colour change (either generally or in certain species) was particularly evident. They are by no means comprehensive but are intended to draw attention to survival strategies. Many areas showed little or none of the effects described here, confirming the observations of Hnatiuk and Hopkins on the patchiness of drought effects.

Dates given below are for 2001 unless stated otherwise.

Sites visited in previous years

Mt Lesueur (ca. 30°10' S, 115°15' E). Valleys and slopes north-east of Mt Lesueur, with varied kwongan. Visited 27 March 1977. Rainfall at Badgingarra for the period 1 October 1976 to 30 April 1977 totalled 55.6 mm, of which 48.0 mm fell in October-November, *i.e.* December to April rainfall was 7.6 mm. Populations of *Petrophile seminuda* and *Melaleuca radula* showed marked colour change.

Location 19769, ca. 15 km S of Corrigin (32°31' S, 117°56' E). Woodland, tall shrubland and kwongan on sand, clayey sand and laterite (George & Hnatiuk 1978). Visited 8 April 1977. Rainfall at Corrigin for the period 1 October 1976 to 30 April 1977 totalled 97.7 mm, of which 59.0 mm fell in October-November and 18.5 in April, *i.e.* December to March rainfall was 20.2 mm.

Hopkins Reserve, SE of Kulin, formerly reserve no. 13389, now 35134 (32°43' S, 118°17' E). A complex area of kwongan, mallee and woodland on sand, sandy loam and laterite. Visited 8 April 1977. For rainfall *cf.* previous site; Corrigin is ca. 55 km to the north-north-west of Hopkins Reserve.

Little Darkin Swamp area (ca. 32°04' S, 116°32' E). Visited 26 April 1994 at the end of a very dry summer/autumn. Varied landforms and vegetation, mainly lateritic gravel and clay-loam with woodland of *Eucalyptus wandoo*, *E. accedens*, *E. calophylla*, some sandy areas carrying *Banksia attenuata* woodland, and granite outcrops. Rainfall at Beverley for the period 1 October 1993 to 30 April 1994 was 30.8 mm, of which 24 mm fell in October and November.

Sites visited in 2001

'First effective rain' refers to the first fall above 10 mm after 1 January 2001 at the recording station closest to the site.

Naval Base, S of Fremantle (32°10' S, 115°46' E). This is a coastal site with low heath and tall shrubland, in sand over Tamala Limestone which outcrops frequently. Visited 7 April, 11 May, 5 June and 10 July. First effective rain 6 May (20 mm).

Cantonment Hill, Fremantle (32°02' S, 115°45' E). This is a low hill of Tamala Limestone near the centre of Fremantle with shrubland of *Acacia xanthina*, *Templetonia retusa*, *Spyridium globulosum*, and some open areas with *Desmodium flexuosus*, exotic grasses etc. Visited 7 April and 20 May. First effective rain 6 May (20 mm).

Kings Park, Perth (31°57' S, 115°50' E). This is the Tamala Limestone escarpment facing the Swan River, just east of where the Crawley swimming baths were located. The vegetation is tall shrubland dominated by *Dryandra sessilis* var *cygnorum*, *Melaleuca huegelii*, *Templetonia retusa* and *Grevillea preissii*. Visited 26 April and 6 July. A number of plants of *Dryandra* and several *Templetonia* and *Dodonaea hackettiana* died. First effective rain 6 May (17.8 mm).

Rottneet Island (32°00' S, 115°31' E). Here, coastal dunes and low hills of Tamala Limestone carry low shrubland of *Acacia*, *Leucopogon*, *Acanthocarpus*, *Olearia*, *Rhagodia*, *Westringia* etc. Visited 6 April. First effective rain 6 May (24.0 mm).

Crystal Brook, Darling Scarp (32°01' S, 116°02' E). This site is on the Darling Scarp east of Perth. There are granitic outcrops on lateritic gravel slopes. Vegetation is mixed low shrubland with occasional *Eucalyptus wandoo* and thickets of mixed Proteaceae, Myrtaceae, Papilionaceae, *Acacia*, *Hibbertia* etc. Around the granite rocks is low herbfield with *Borya*, *Stylidium*, ephemerals and scattered small shrubs such as *Verticordia huegelii*. Visited 27 March 1997, 15 March 2001, 4 May, 17 May, 22 May, 5 July and 7 August. First effective rain 6 May (28 mm). In 2001, large areas assumed an orange aspect as shrubs went dormant or died. Some remained green, e.g. *Hakea incrassata*, many *Hakea trifurcata*. Deaths occurred in *Nemcia spathulata*, *Hakea incrassata*, *Hakea erinacea*, *Hakea trifurcata*, *Acacia pulchella*, *Dryandra lindleyana*, *Casuarina humilis*, *Gonocarpus*, *Jacksonia*, *Pimelea imbricata*, *Calytrix glutinosa*, *Petroplile biloba*, *Hovea pungens*, *Verticordia acerosa*, *Eucalyptus wandoo*. By 5 July regreening had occurred and a 'normal' aspect resumed apart from the many dead shrubs.

Lewis Rd, Forrestfield, Darling Scarp (32° 00' S, 116° 02' E). This site is similar to the preceding but with doloritic rocks; there are granitic outcrops higher on the Scarp. Visited 4 May, 5 July and 7 August. In 2001, deaths occurred in *Nemcia spathulata*, *Hakea trifurcata*, *Hakea lissocarpa*, *Acacia pulchella*, *Dryandra lindleyana*, *Daviesia divaricata*. By 5 July regreening had occurred and a 'normal' aspect was resumed apart from the many dead shrubs.

Hummerston Road, Piesse Brook, E of Kalamunda (31° 58' 30" S, 116° 04' 30" E). This is a gently sloping granitic outcrop surrounded by open woodland of *Eucalyptus*

wandoo with a mixed understorey. Visited 27 March 1997, 22 May 2001 and 5 July. First effective rain 6 May (28 mm).

Seabird, S of Lancelin (31° 16' S, 115° 27' E). Coastal dunes immediately north of the caravan village; a low rise of Tamala Limestone just east of the road with low kwongan, and another rise with sand over limestone at the entrance to the rubbish tip about a kilometre further north, with kwongan and tall shrubland. Visited 22 April, 1 June and 11 July. First effective rain 6 May (25.8 mm).

near Minyolo Brook, Brand Highway (30° 42' S, 115° 30' E). A sandy flat on the east side of the highway with low kwongan dominated by *Gastrolobium oxylobioides*, *Daviesia angulata*, *Calothamnus sanguineus*, *Isopogon divergens*, *Hakea trifurcata*, *Hibbertia hypericoides*, *Ecdeiocolea monostachya* and *Caustis dioica*. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

corner Mullering Road & Brand Highway (30° 41' S, 115° 28' E). Deep sand with low open woodland of *Banksia attenuata*, *B. menziesii*, *Adenanthos cygnorum* and mixed understorey. Visited on 1 April and 27 May. First effective rain 6 May (22 mm).

ca 1 km S of Tiwest Mine turnoff, Brand Highway (30° 39' S, 115° 28' E). A winter-wet clay depression on E side of road with open shrubland of *Melaleuca viminea* subsp *viminea*, *Casuarina microstachya* and *Hakea trifurcata*, interspersed with low herbfield of *Borya*, *Conostylis* etc. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

S of Badgingarra, Brand Hwy (30° 33' S, 115° 28' E). Shallow sand over laterite high on rise (near *Eucalyptus pendens*), with species-rich low kwongan. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

Hill River bridge, Brand Hwy (30° 20' 20" S, 115° 28' 30" E). This site, immediately south of the bridge, is a clay-loam flat with low kwongan. *Petroplile seminuda* is common here and has been recorded with red foliage in several years, e.g. autumn 1969. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

Boothendarra Creek, Brand Hwy (30° 17' S, 115° 29' E). Flat area with heath of *Thryptomene mucronulata*, *Melaleuca viminea* subsp *viminea* and *Ecdeiocolea monostachya*. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

S of Coomallo Creek, E side of Brand Hwy (30° 15' S, 115° 27' E). A clay-loam flat with heath of *Thryptomene mucronulata*, occasional *Calothamnus* (which remained green), and a thicket of *Casuarina campestris*, *Melaleuca platycalyx*, *Acacia multispicata* and *Petroplile seminuda*. Visited 1 April and 27 May.

N of Coomallo Creek, Brand Hwy (30° 12' 30" S, 115° 23' 30" E). A high lateritic rise with species-rich low kwongan. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

Marchagee Track, between Coomallo and Gunyidi (30° 07'-12' S, 115° 35'-50' E). Several locations with kwongan and tall shrubland on sand or sandy loam. Visited 1 April and 27 May. First effective rain 6 May (22 mm at Badgingarra, 10 mm at Watheroo).

Pinjarrega Lake Nature Reserve (30° 07' S, 115° 59' E). On the Marchagee Track near the south-eastern corner of

the reserve, clay-loam with open *Eucalyptus loxophleba* and *Melaleuca* sp, and an open ground layer of perennial monocots such as *Triodia danthonioides*, *Conostylis aculeata* subsp *bromelioides* and *Harperia lateriflora*. Visited 1 April and 27 May. First effective rain 6 May (10 mm at Watheroo).

N of Moora (30° 33' S, 116° 02' E). Western side of Cairne Hill, on a low quartzite ridge dominated by *Casuarina campestris*, with occasional *Acacia acuminata* open woodland on the adjacent flat. Visited 1 April and 27 May. First effective rain 6 May (10 mm).

Charles Gardner Flora Reserve, S of Tammin (31° 47' S, 117° 28' E). Visited 10 March, 7 June and 19 August. Effective rain at Tammin in 2001: 11 January (11 mm), 21 January (30 mm), 24 February (11 mm), 23 April (24 mm), 31 May (17 mm). During May, rain of 1-7 mm was also recorded on 12 other days between 6th and 30th. Summer rainfall over the reserve was probably much less, a farm adjacent on the southern side having received ca. 15 mm in January and February in contrast to just over 60 mm in

the town (W Gardner, personal communication). Observations were made at three sites: 1, on a sandy rise towards the southern edge with scattered *Casuarina huegeliana*, *C. campestris*, Cyperaceae, *Santalum spicatum*, *Acacia merinthophora* etc.; 2, an area of tamma scrub on sandy loam along the western edge dominated by *Casuarina campestris* with *Verticordia eriocephala*; 3, a high lateritic ridge on the northern edge, with thick mixed scrub dominated by Proteaceae. On 7 June the reserve was still recovering from drought despite there having been some 78 mm of rain since 23 April (after no rain between 25 February and 23 April) and the soil being damp. Most *Schoenus calcatus* were still bright yellow, only a few (maybe 10%) showing clear regreening. Other Cyperaceae were at similar stages, except *Caustis dioica* which generally was green. *Astroloma serratuloides* was fully green and flowering. *Conostylis petrophiloides* had regreened, but many *Dryandra purdieana* still had yellowish or orange leaves. On 19 August the vegetation was generally fully green and in good condition, although flowering was just starting. *Dryandra speciosa*

Table 1.

Rainfall (mm) for localities nearest those where observations were made in 2001. An effective rain event is here taken as at least 10 mm within a 24-hour period. Note that for Swanbourne, Perth, Rottnest and Bickley, more than half of the rain for the period 1 October 2000 to 30 April 2001 fell during November. Tammin received effective falls in January, February and April. In the average annual rainfall column the second figure is the number of years for which there are recordings.

Locality	Average annual rainfall	Total rainfall in 2000	Average rainfall, 1 Oct to 30 April	Rainfall, 1 Oct 2000 to 30 April 2001	First effective rain event, 2001	Rainfall from then until 31 May 2001
Badgingarra Research Stn	572.8 39 years	274.4	134.4	21.0	6 May 22.0	108.2
Swanbourne	773.8 16 years	748.6	126.5	57.7	6 May 20.0	139.0
Perth	799.1 8 years	796.2	144.5	48.8	6 May 17.8	108.8
Lancelin	626.0 35 years	485.0	126.9	41.0	6 May 25.8	117.3
Bickley	1095.6 99 years	1192.2	241.5	63.8	6 May 28.0	146.2
Watheroo	423.5 99 years	352.2	111.6	26.0	6 May 10.0	47.8
Moora	464.1 99 years	376.6	118.7	19.6	1 Mar. 12.0 6 May 10.4	58.8
Rottnest	584.6 6 years	477.8	140.4	36.8	6 May 24.0	144.0
Tammin	345.5 89 years	346.3	114.4	100.6	19 Jan. 11.0 21 Jan. 30.6 24 Feb. 11.0 23 Apr. 24.4	143.0
But see discussion in text						

appeared to have had no flowers during its usual season (July–August), and *D. purdieana* had few flowers.

Results

Below are species in which I recorded the foliage changing colour, then regreening. Nomenclature follows Paczkowska & Chapman (2000) except that *Casuarina* is accepted instead of *Allocasuarina*. The list is alphabetical under families, with Dicotyledons followed by Monocotyledons. Dicots are shrubs unless noted otherwise. Monocots are all rhizomatous perennial herbs. Where known, species are described as seeders (*i.e.* killed by fire, regenerate from seed) or sprouters (having a lignotuber, rhizome or similar storage organ and sprouting from this after fire). Leaf orientation and texture remained normal except as indicated otherwise. The date when species were recorded as regreened is that when a site was visited; plants may have been regreened before that date.

Dicotyledons

Casuarinaceae

Casuarina campestris Diels. Seeder, dioecious. A characteristic 'autumn' plant even in normal summers, commonly seen (both sexes) various shades of gold, brown or red-brown during late summer and autumn, *e.g.* Avon Location 19769 (S of Corrigin) 8 April 1977; Hopkins Reserve 35134, SE of Kulin, 8 April 1977; near Manmanning 8 February 1980; near Meenaar (W of Meckering) 27 February 1994. In 2001 brown at Charles Gardner Reserve on 10 March, regreened on 7 June; N of Moora, quite brown 1 April, partly regreened 27 May; S of Coomallo, brown or golden 1 April, regreened 27 May. Mentioned by Main (1967).

Casuarina huegeliana Miq. Seeder, dioecious. Foot of Crystal Brook hill: a number of trees (both sexes) brown 15 March, regreened 22 May.

Casuarina humilis Otto & F Dietr. Sprouter, dioecious. Crystal Brook: a number of plants (both sexes) turned pale purple or pink (27 March 1994, 15 March 2001) and regreened after rain 17 May 2001. Kings Park: stems pinkish brown 26 April.

Casuarina microstachya Miq. Seeder, dioecious. S of Tiwest Mine turnoff, Brand Hwy: branchlets (both sexes) yellow 1 April; regreened 27 May.

Dilleniaceae

Hibbertia hypericoides (DC) Benth. Sprouter. In 2001, plants at a number of localities (*e.g.* Seabird, Crystal Brook, Naval Base, Kings Park, Yanchep) generally turned golden or brown. Regreening took several weeks but generally was completed by 31 May. Plants had commenced flowering at Naval Base on 10 July and at Seabird on 11 July.

Hibbertia spicata subsp. *leptotheca* J R Wheeler. Naval Base: leaves yellow 7 April; still mostly yellow 11 May; regreened 5 June; inflorescence growth started 10 July.

Epacridaceae

Astroloma serratifolium (DC) Druce. Seeder. Charles Gardner Reserve: leaves pale green 10 March; regreened and flowering 7 June.

Leucopogon conostephioides DC. Seeder. Boothendarra Creek: leaves yellowish 1 April.

Leucopogon insularis DC. Seeder. Seabird: leaves yellowish, occasionally red, and resting flower buds present, 22 April; green and plants flowering 1 June; flowering over, new vegetative growth 11 July. Rottneest ls: leaves yellow 6 April; not followed up.

Leucopogon parviflorus (Andrews) Lindley Sprouter. Naval Base: leaves yellow 7 April; regreened 5 June; flower buds developing 10 July.

Euphorbiaceae

Phyllanthus calycinus Labill. Sprouter. During summer this species typically loses many leaves and by autumn has few remaining. In 2001 at Crystal Brook, Naval Base and Seabird, the remaining leaves were yellowish. At Crystal Brook, these old leaves had regreened and new shoots were just beginning to develop on 17 May. The process was further advanced at Seabird on 1 June; by 11 July flowering had started there. At Naval Base, old leaves had regreened by 11 May, and by 5 June these had almost all fallen, the new shoots being then well advanced.

Stachystemon axillaris A S George. Seeder. Tathra National Park: leaves yellowish 15 February; not followed up.

Fabaceae

Bossiaea eriocarpa Benth. Sprouter. Seabird: leaves yellow 22 April; not noted on 1 June; regreened 11 July.

Gastrolobium calycinum Benth (York Road Poison). Seeder. Dale, near Little Darkin Swamp: leaves very pale 26 April 1994. Not followed up.

Gastrolobium oxylobioides Benth (Champion Bay Poison). Seeder. Near Minyolo Brook, Brand Hwy: leaves yellowish, 1 April; regreened 27 May.

Gastrolobium spinosum Benth (Prickly Poison). Seeder. Julimar Road, Chittering: leaves pale golden-brown, April 1994. Not followed up.

Gompholobium tomentosum Labill. Seeder. Leaves yellowish (Seabird 22 April, Naval Base 7 April); regreening 11 May (Naval Base), 1 June (Seabird) but some still yellowish.

Hovea pungens Benth. Seeder. Crystal Brook: leaves dull green to yellowish with resting flower buds, 27 March 1997; regreened and buds developing, 22 May 2001; flowering 6 July. Some plants died. One plant noted with one dead branch and one flowering 7 August.

Jacksonia alata Benth. A leafless perennial herb; seeder? Crystal Brook: stems turned yellow. Behaviour after rain varied, some plants regreening over several weeks (22 May), but many died.

Jacksonia sp. A leafless perennial herb; seeder? Charles Gardner Reserve: stems orange 10 March, still so 7 June; regreened 19 August.

Nemcia spathulata (Benth) Crisp. Seeder. Crystal Brook: yellowish, 27 March 1997 and in 2001; green 22 May, but many plants died.

Nemcia reticulata (Meisn) Domin. Seeder. Seabird: variable; leaves orange or green 22 April; regreened and with young buds 11 July; many plants died; one noted on

11 July with about half its branches dead, the others regreened.

Sphaerolobium macranthum Meisn. Seeder. A leafless perennial herb. N of Coomallo: stems golden 1 April; greening 27 May

Templetonia retusa (Vent) R Br. Sprouter. At Seabird, Fremantle and Kings Park: the leaves on most plants turned golden; some plants died. Most regreened after rain, the change becoming evident after 3-4 days and taking up to two weeks to become fully green. Some plants, however, were still yellowish at the end of May. Possibly these were on the verge of death and were slower to regreen. Beyond the dormant stage, the foliage becomes bleached as death sets in. Flowering had commenced at Seabird by 1 June; in full flower at Kings Park 6 July, and Naval Base 10 July. At Seabird there were still flowers on 11 July and the early flowers were already developing fruit; one plant was flowering even though the foliage was still yellowish.

Goodeniaceae

Dampiera sp. A clonal perennial herb; sprouter. Charles Gardner Reserve: many plants had deep reddish leaves and stems on 10 March and were similar on 7 June, but most had regreened by 19 August. Some reddish colouring may be normal, especially in ageing leaves.

Lamiaceae

Hemianandra glabra Benth subsp *glabra*. Seeder. Some plants at Seabird were yellowish on 22 April. On 1 June most were healthy green, but a few remained yellowish.

Hemigenia incana (Lindl) Benth. Seeder. Crystal Brook: most plants were dormant on 15 March, the leaves pale green and commonly slightly pink towards the margins which were a little more inrolled than usual. In some plants the leaves were brittle and brown with the appearance of death. On 22 May most were regreened and soft; most fully regreened 6 July. Some plants shed leaves but resprouted, others died.

Westringia dampieri R Br. Seeder. Rottneest Island: foliage golden 6 April. 2001.

Mimosaceae

Acacia acuminata Benth. Small tree; seeder; phyllodinous. N of Moora: mature trees with dull yellowish-green phyllodes 1 April; regreened 27 May.

Acacia lasiocarpa Benth var *lasiocarpa*. Seeder; bipinnate leaves. Seabird: leaflets quite yellow and inrolled 22 April; regreened and with bright green new growth 1 June; in bud 11 July. Plates 1, 2.

Acacia multispicata Benth. Seeder; flat-phyllode variant. Non-lignotuberous. Boothendarra Creek: phyllodes yellow 1 April; some fully green on 27 May, others still yellowish.

Acacia pulchella R Br var *pulchella*. Seeder; bipinnate leaves. Crystal Brook: leaflets yellow, closed together and rachis turned downwards 27 March 1997 and 15 April 2001; regreened and expanded 22 May 2001. Many plants died.

Acacia truncata (Burm f) Hoffmanns. Seeder; triangular phyllodes. Seabird: variable; on 22 April, some were green, others were yellowing; all green 1 June.

Myrtaceae

Baeckea crispiflora F Muell. Seeder. Charles Gardner Reserve: leaves reddish 10 March; regreened 7 June.

Baeckea aff *preissiana* (Schau) Domin. Seeder. Dale, near Little Darkin Swamp: leaves yellow to golden brown or orange 26 April 1994; not followed up.

Calothamnus torulosus Schauer. Sprouter. N of Coomallo: variable; a number of plants with pale purplish or pink foliage 1 April; regreened 27 May. Crystal Brook: some plants with pink or pale purple foliage 15 April; regreened 6 July.

Calytrix glutinosa Lindl. Seeder. Crystal Brook: leaves yellow, somewhat appressed 15 April; regreened 22 May but some plants were dead; surviving plants with new vegetative growth 5 July. A sticky white exudate appeared around the new shoots, apparently similar to that seen on species of *Eremaea*.

Darwinia citriodora (Endl) Benth. Seeder? Crystal Brook: leaves turned shades of red or pale purple March 1997 and 15 April 2001; regreening 22 May; fully regreened 6 July.

Darwinia speciosa (Meisn) Benth. Sprouter? N of Coomallo: foliage reddish 1 April; regreening but only a little on 27 May.

Darwinia aff *nieldiana* F Muell. Seeder. Marchagee Track: variable, but a number of plants quite yellow on 1 April; regreening 27 May.

Hypocalymma angustifolium (Endl) Schauer. Sprouter. Crystal Brook: leaves reddish 27 March 1997; dull green 18 April 2001; regreened and flower buds developing 6 July.

Melaleuca elliptica Labill. Seeder. Dragon Rocks Reserve, SSE of Hyden: leaves deep pink on upper surface but remained greenish below 18 April 2001 (M Pieroni, personal communication).

Melaleuca platycalyx Diels. Seeder. Boothendarra Creek: leaves pinkish grey with red-brown margins 1 April; regreening 27 May (margins remain brownish).

Melaleuca radula Lindl. Sprouter. NE of Mt Lesueur: leaves yellow 27 March 1977. Crystal Brook: leaves becoming grey 15 March; still so 22 May, and many leaves appearing dead; by 5 July, some leaves had regreened, and new shoots were developing at the lignotuber and along older stems on some plants with dead leaves. The new growth was farther advanced on 7 August, with some flower buds developing.

Melaleuca urceolaris F Muell ex Benth. Boothendarra Creek and S of Coomallo: leaves yellow and the oldest ones brown, with persistent dead flowers from previous year 1 April; regreening 27 May.

Melaleuca viminea Lindl subsp *viminea*. Seeder? S of Tiwest Mine turnoff, Brand Hwy, and S of Coomallo: leaves yellowish 1 April; fully regreened 27 May.

Thryptomene mucronulata Turcz. Seeder. Boothendarra Creek: leaves red-brown 1 April; regreened 27 May. Plates 3, 4.

Verticordia acerosa Lindl var *acerosa*. Seeder. Crystal Brook: stem and floral leaves yellow or brown 15 March; regreened 22 May but some plants dead.

Verticordia chrysanthella A S George. Sprouter. A group planted at the Western Australian Herbarium Kensington, regularly turns brown during the summer and regreens with the first autumn rain. Unseasonal summer rain, as occurred in January 2000, also causes regreening.

Verticordia eriocephala A S George. Seeder. Charles Gardner Reserve: leaves yellowish-green 10 March; regreened 7 June.

Verticordia huegelii Endl var *huegelii*. Seeder. Crystal Brook: leaves red 15 March; regreening 22 May; fully regreened 5 July; new growth 7 August. Some plants died.

Verticordia huegelii var *decumbens* A S George. Sprouter. Hummerston Rd, Piesse Brook: leaves reddish 27 March 1997; not observed again 1997. Regreening 22 May 2001, and a number of plants appearing dead; most surviving plants fully regreened 5 July, some with new leaves developing among dead ones.

Proteaceae

Conospermum huegelii Endl. Perennial herb; seeder. Crystal Brook and Hummerston Rd, Piesse Brook: this species normally has pale green foliage, but it appeared to be even paler during late summer (27 March 1997, 15 April 2001), regreening after the first rains (22 May 2001). Some plants died.

Dryandra purdieana Diels. Seeder. Charles Gardner Reserve: many plants with yellow and orange leaves 10 March; similar 7 June; mostly regreened 19 August.

Grevillea endlicheriana Meisn. Sprouter. Crystal Brook: leaves turning brown 15 March, 15 April; on 22 May many plants appeared dead, with grey leaves; on 10 July some plants appeared dead, on others leaves had regreened, and on some new shoots were developing either from stems or the lignotuber.

Isopogon scabriusculus Meisn subsp *scabriusculus*. Seeder? Charles Gardner Reserve: leaves dull to pale green, 10 March; regreened 7 June. The colour change was subtle.

Petrophile seminuda Lindl. Seeder. A characteristic 'autumn' plant, recorded red at various localities, e.g. Mt Lesueur 27 March 1977; near Meenaar (W of Meckering) 27 Feb 1994; West Dale area (near Little Darkin Sump) 26 April 1994; Hill River bridge, Brand Hwy 1 April 2001; Charles Gardner Reserve, 7 June. Regreened at Charles Gardner 19 August; regreened and flowering at Hill River bridge 5 September.

Petrophile squamata R Br. Seeder. Tootbardi Road: leaves deep red, 27 March 1977.

Stirlingia abrotanoides Meisn. Seeder? N of Coomallo, Brand Hwy: in this small shrub the leaves became slightly paler than usual and the lobes closed together somewhat (1 April), 'regreened' and returned to normal 27 May.

Stirlingia simplex Lindl. Seeder? A small shrub with very soft, finely divided foliage that remains soft and turns pink or mauve as summer progresses, e.g. Dale (near Little Darkin Swamp) 26 April 1994; generally regreens with winter rain but in a few plants the pink tinge persists (Dale, 19 August 2001).

Synaphea spinulosa (Burm f) Merrill. Sprouter. Tootbardi Rd: leaves yellowish 27 March 1977; Charles Gardner Reserve: leaves yellowish 10 March; still so 7 June; regreened 19 August. In this genus the foliage of many species characteristically has a yellow tinge, but in some this becomes more pronounced during autumn.

Synaphea sp. Seeder. Reserve 19486: leaves yellowish 8 April 1977; not observed later.

Rhamnaceae

Spyridium globulosum (Labill) Benth. Seeder. Naval Base: leaves yellowish 7 April, regreened 11 May; in full flower 10 July. Cantonment Hill: leaves yellowish 7 April, regreened 20 May. Seabird: leaves of some plants yellowish 22 April; regreened 27 May, in full flower 11 July. In this species many leaves have damaged parts, of various brown or reddish shades. Some plants at Seabird died in autumn 2001.

Trymalium ledifolium var *rosmarinifolium* (Steud) Benth. Seeder. Crystal Brook: leaves pale, dull green or yellowish and somewhat appressed 15 March; still yellowish 17 May; regreened and flowering 5 July; Hummerston Rd, Piesse Brook: leaves pale green or slightly yellow 27 March 1997; not observed again in 1997, but green 22 May 2001.

Rutaceae

Boronia alata Sm. Seeder. On Rottnest Island the foliage turned red in autumn 2001 (G J Keighery, Wildlife Research Centre, personal communication).

Philotheca spicata (A Rich) Paul G Wilson. Sprouter. Naval Base: leaves somewhat yellowish 7 April; regreened 10 July.

Santalaceae

Leptomeria empetrifomis Miq. Like many of its family, both the stems and leaves of this semi-parasitic plant are usually yellowish green or somewhat reddish. At Seabird on 22 April they were quite an intense red, but changed to yellowish after rain (1 June); most were regreened by 11 July but the stems remained reddish.

Sapindaceae

Dodonaea aptera Miq. Seeder. Cantonment Hill: leaves dull, dormant flower buds present 7 April; leaves soft, fully green, and plants in flower 20 May.

Dodonaea hackettiana W Fitzg. Seeder. Kings Park: leaves dull, pale green or straw-colour with some plants appearing dead 26 April; most fully regreened 6 July but one plant dead.

Sterculiaceae

Thomasia cognata Steud. Seeder? Naval Base: leaves yellowish 7 April; regreening variably 11 May; fully regreened 5 June.

Thomasia macrocarpa Endl. Seeder. Crystal Brook: leaves yellow or pale green and hanging more steeply than usual 15 March; not noted in May; regreened and spreading, with new growth and buds 7 August.

Lasiopetalum drummondii Benth. Sprouter. N of Coomallo: leaves yellow-brown 1 April; some regreened and some still yellowish 27 May.



Plate 1. *Acacia lasiocarpa* at Seabird, 22 April 2001. Leaflets tightly rolled and closed together.



Plate 2. *Acacia lasiocarpa* at Seabird, 1 June 2001. Leaflets unrolled, spreading.



Plate 3. *Thryptomene mucronulata* at Boothendarra Creek, Brand Highway, 1 April 2001.



Plate 4. *Thryptomene mucronulata* at Boothendarra Creek, Brand Highway, 27 May 2001.



Plate 5. *Pimelea ferruginea* at Seabird, 22 April 2001. Leaf margins revolute; old flowers present.



Plate 6. *Pimelea ferruginea* at Seabird, 1 June 2001. Leaves almost flattened; flowers fallen; new shoots right.



Plate 7. *Schoenus calcatus* at Charles Gardner Reserve, south of Tammin, 10 March 2001.



Plate 8. *Schoenus calcatus* at Charles Gardner Reserve, south of Tammin, 7 June 2001.

Thymelaeaceae

Pimelea ferruginea Labill. Seeder. Seabird: leaves yellow with margins more revolute than usual 22 April; fully regreened and margins less revolute, some with vigorous new growth 1 June. Flowered well September-October 2001. Plates 5, 6.

Pimelea imbricata var *piligera* (Benth) Diels & E.Pritzel. Seeder. Crystal Brook and Hummerston Road. In this small shrub the leaves became grey and folded lengthwise. After rain some leaves regreened, with new shoots developing 22 May; new leaves further developed 5 July. During 2000-2001 some plants died.

Tremandraceae

Tetralthea confertifolia Steetz. Sprouter; perennial herb. N of Coomallo: leaves reddish 1 April; partly regreened 27 May.

Tetralthea sp. Seeder? A leafless perennial herb. Charles Gardner Reserve: stems orange 10 March.

Monocotyledons

Boryaceae

Borya sphaerocephala R Br. The classic resurrection plant of Western Australia. Leaves commonly turn orange from late spring until the first rains of autumn or winter. Abnormal summer rain causes regreening. Gaff (1981) recorded maintaining plants in the dormant state for 5 years [as *B. nitida* Labill]. Some populations turn straw-colour, e.g. at Charles Gardner Reserve 10 March 2001. A common species around granitic rocks in the Darling Range near Perth and farther inland.

Borya constricta Churchill. Occurs farther inland than *B. sphaerocephala* and generally turns a richer orange when stressed. Recorded e.g. at Mouroubra Station (S of Paynes Find) 19 April 1976; N of Merredin 10 March 2001.

Two south-western species of *Borya* (*B. laciniata*, *B. scirpoidea*) are drought avoiders, being deciduous or almost so during the summer, though the old inflorescences persist. Growth of new leaves begins immediately after the first rain falls in autumn.

Cyperaceae

Caustis dioica R Br. Sprouter. Dale, near Little Darkin Swamp: culms yellow 26 April 1994. Minyolo Brook, Brand Hwy: culms yellow 1 April 2001; regreened 27 May. Charles Gardner Reserve: culms yellow 10 March; regreened or yellow-green, 7 June; all regreened 19 August.

Lepidosperma sp. Sprouter? A robust plant with flattened culms. Hopkins Reserve, SE of Kulin: culms yellow 8 April 1977.

Lepidosperma sp. Sprouter? A robust plant with terete stems. Hummerston Rd, Piesse Brook: culms yellow-green, 27 March 1997.

Lepidosperma sp. Sprouter? A robust plant with slender flat stems. Crystal Brook: stems yellow 15 March; green 5 July.

Mesomelaena stygia (R Br) Nees. Sprouter? Charles Gardner Reserve: culms green or yellowish 10 March; still yellowish to green 7 June; regreened, some flowering 19 August.

Schoenus aff *brevisetis* (R Br) Roem & Schult. Seeder? Charles Gardner Reserve: culms pale yellowish-green 10 March; still somewhat yellow 7 June; regreened 19 August.

Schoenus calcatus K L Wilson. Seeder? Avon Location 19769: culms and leaves golden yellow 8 April 1977. Charles Gardner Reserve: bright yellow or yellow-orange 10 March; some plants half-green, others still yellow 7 June; all regreened 19 August. The mechanism in this species may be similar to that of *Borya*, i.e. a breakdown of the leaf cell structure, followed (after wetting) by regreening with reconstitution of the structure and resumption of normal functions. The time taken to regreen seems to be much longer. Plates 7, 8.

Schoenus aff *clandestinus* S T Blake. Seeder? S of Badgingarra: leaves golden 1 April; regreening 27 May.

Dasypogonaceae

Calectasia narragara R L Barrett & K W Dixon. Sprouter. N of Coomallo: leaves yellowish, 1 April; regreened 1 June.

Lomandra maritima T S Choo. Sprouter. Seabird: leaves orange 27 April; regreened 1 June.

Ecdeiocoleaceae

Ecdeiocolea monostachya F Muell. Sprouter. Near Minyolo Brook and Boothendarra Creek: culms orange or yellow 1 April; regreened 1 June. Mentioned by Main (1967).

Haemodoraceae

Conostylis aculeata subsp *breviflora* Hopper. Seeder. Boothendarra Creek: leaves yellowish 1 April.

Conostylis aculeata subsp *bromelioides* (Endl) J Green. Seeder? Pinjarrega Lake Reserve: leaves golden or brown 1 April; on 27 May some plants had green foliage, but others were brown and appeared dead.

Conostylis pauciflora subsp *euryrhipis* Hopper. Seeder? Seabird: leaves pale yellow 27 April; green 1 June.

Conostylis petrophiloides F Muell ex Benth. Seeder. Charles Gardner Reserve: leaves golden 10 March; green 7 June.

Poaceae

Triodia danthonioides (F Muell) Lazarides. Seeder. Pinjarrega Lakes Nature Reserve: leaves orange on 1 April; regreened 27 May (note: this plant has many old dead leaves in its 'normal' mature state).

Restionaceae (data on seeders/sprouters from Meney & Pate 1999)

Alexgeorgea subterranea Carlquist. Seeder. S of Badgingarra: many plants with yellow culms 1 April 27; those near road had regreened by 27 May, but those in undisturbed vegetation remained yellowish.

Catacolea enodis B G Briggs & L A S Johnson. Seeder. S of Badgingarra: culms yellow 1 April; regreened 27 May.

Desmocladus flexuosus (R Br) B G Briggs & L A S Johnson. Sprouter. Naval Base, Cantonment Hill: culms yellow 7 April; regreening 11 May (Naval Base); fully regreened 20 May (Cantonment Hill), 10 July (Naval Base).

Desmocladus parthenicus B G Briggs & L A S Johnson. Seeder. Marchagee Track: culms and branchlets yellow 1 April; regreened 27 May

Harperia lateriflora W Fitzg. Sprouter. Pinjarrega Lake Reserve: culms very pale green 10 March; fully green 7 June

Lepidobolus quadratus B G Briggs & L A S Johnson. Seeder. N of Coomallo: culms pale green or yellowish 1 April; regreened (with a blue tinge) 27 May.

Other drought strategies

Deciduousness and protection by dead leaves

Alyogyne huegelii (Endl) Fryxell (Malvaceae). At Seabird in 2000-2001 this shrub had shed all or most leaves by 22 April, the stems generally turning deep red. A very few surviving leaves remained green. On 1 June new shoots were developing. The stems either remained red or turned somewhat green. In full leaf, with mature flower buds 27 September.

Opercularia spermacoea Juss (Rubiaceae). At Seabird, the leaves of this perennial herb were dead (dark grey, brittle) on 22 April but the stems remained green. On 1 June new shoots were developing; by 11 July flowering had started. The old leaves persist for at least a year, i.e. are not deciduous immediately.

Opercularia vaginata Juss (Rubiaceae). This suckering perennial herb is almost deciduous in summer. At Seabird, it was slower to develop new leaves than *S. spermacoea*. New shoots and early flowers, Charles Gardner Reserve, 19 August.

The semi-deciduous habit of *Phyllanthus calycinus* is described above.

Several perennial herbs were recorded in which the leaves die during summer but form a protective cover over the stems and/or rootstock. These include species of stilt plants, e.g. *Laxmannia squarrosa* Lindl (Anthericaceae) and *Stylidium bulbiferum* Benth and other species (Stylidiaceae) at Hummerston Road and Crystal Brook. The phenology of stilt plants was described by Pate *et al.* (1984), but they reported no death or colour change in the foliage, only slow growth or even a decrease in dry weight during summer and autumn. According to the rainfall figures that they cited, during the summer of 1980-81 when their study was made there was effective rain in January and March, hence the plants were not subject to a long summer drought.

In *Laxmannia squarrosa*, the leaves in a population at Hummerston Rd, Piesse Brook, turned yellow 27 March 1997 but were not observed again that year. In 2001, new leaves were present on 22 May, those of the previous year appearing dead. The dead leaves are not deciduous immediately but seem to persist for at least a year.

Schoenus aff clandestinus S T Blake (Cyperaceae). At Charles Gardner Reserve the leaves of this very small cushion sedge died, turned white and curled up, providing a protective covering to the rhizome (10 March). On 19 August new leaves were well developed and most old leaf laminas had fallen.

Sacrificing parts

From observations made in autumn 2001 I suggest that another strategy for surviving drought is the sacrifice of

foliage or whole branches. In several species, parts of plants died and the remainder survived. In *Eucalyptus wandoo* Blakely (Myrtaceae) at Crystal Brook and Forrestfield, most trees showed no or little drought effect, but the foliage died on a number of young plants (up to 4 m tall). In some of these a very few leaves remained green. On 7 August some of these plants had new epicormic shoots and appeared to have survived as they do after fire. These will be monitored to see whether they return to normal growth.

At Crystal Brook a plant of *Hovea pungens* lost one major stem but the other survived and flowered. Likewise, at Crystal Brook and Forrestfield, many plants of *Melaleuca radula*, *Grevillea endlicheriana* and *Hemigenia incana* showed this strategy. One plant of *Nemcia reticulata* was also noted at Seabird with half its branches dead, the remainder green.

In autumn 2001, many *Xanthorrhoea preissii* Endl (Xanthorrhoeaceae) at several localities (e.g. Forrestfield, Crystal Brook, Badgingarra) seemed stressed, the lower leaves and/or upper parts of leaves turning yellow. These parts did not regreen after rain.

Colour change in bark

Seasonal change in the colour of bark is well-known in some smooth-barked species of *Eucalyptus* (Brooker & Kleinig 1990). An outstanding example is *E. erythronema* Turcz in which the newly exposed bark is silver or white but gradually changes to deep red before peeling in autumn. The pastel pink or orange tones of *E. accedens* W Fitzg and *E. salmonophloia* F Muell also intensify during autumn, then become pale again during winter.

Discussion

One question that I have addressed is what term to adopt for the strategy of colour change and its reversal. Gaff (1981) and others have used 'resurrection plant' for *Borya* and other species but I believe that few of the species reported here have the ability to remain in the non-green state for several years, as is the case with resurrection plants, although *Schoenus calcatus* is an obvious candidate. Dormancy seems inappropriate, since it usually refers to a normal seasonal reduction in metabolism to a steady low state, e.g. as a seed or as a deciduous plant. Aestivation is used for animals that assume a low metabolic rate or torpor during summer (cf. hibernation), but in botany refers to the arrangements of floral parts and hence its use with another meaning would cause confusion. Ferns that can reduce their water content to a low level and recover have been described as desiccation-tolerant. The condition I am describing does not occur to the same degree every season, varying in response to current conditions. It may be reversed by abnormal rainfall, in contrast to typical dormancy that awaits a change in season (especially in day length or temperature). Quiescence also seems inappropriate, since a plant may be quiescent metabolically but not show outward symptoms as we have here. To describe the strategy of plants that show a reduction in metabolic rate indicate by change in colour of vegetative parts and then revert to the green state I am proposing the term *diallagy* (adj *diallagous*). This is derived from the Greek *diallage* (interchange).

Diallagy is generally indicated by a change in colour of the foliage. At first glance the plants may appear dead, but with experience one can usually distinguish between those still alive and those that have died (the latter commonly shown by a grey colour). A wide range of colours develops: brown, purple, red, yellow, orange. These are what I call our autumn colours. Most are more subtle than the brilliant colours of deciduous trees of the Northern Hemisphere, and of course they are not associated with leaf fall, but nonetheless they are quite evident. Once you become attuned to the condition you begin to see how widespread it is both taxonomically and geographically. I have, however, been tricked by plants that appeared dead but later regreened, e.g. several *Dodonaea hackettiana* in Kings Park, *Hemigenia incana* at Crystal Brook. A rule of studies in diallagy should be to always check after the rains come!

Table 2

Families in which diallagy is reported.

Dicotyledons	Monocotyledons
Casuarinaceae	Boryaceae
Dilleniaceae	Cyperaceae
Epacridaceae	Dasypogonaceae
Euphorbiaceae	Ecdeicoleaceae
Fabaceae	Haemodoraceae
Goodeniaceae	Poaceae
Lamiaceae	Restionaceae
Myrtaceae	
Proteaceae	
Rhamnaceae	
Rutaceae	
Santalaceae	
Sapindaceae	
Thymelaeaceae	
Tremandraceae	

The texture of diallagous leaves tends to remain similar to that of the leaves in the green state. In some cases there is also an appearance of being slightly shrivelled but, given the sclerophyllous form of the leaves of most species in our flora, the latter is uncommon. In a few species leaf orientation changes, e.g. in *Acacia lasiocarpa* and *Acaica pulchella* where the rachis bends downwards, the pinnae close on the rachis and the leaflet margins become more tightly revolute. In *Hemigenia* and *Thomasia* the leaves may bend downwards slightly at the petiole.

The condition is highly variable in its expression. Sometimes it appears in whole populations, sometimes only in individual plants. A plant in the coloured state may occur close to one that appears normally green.

Diallagy is here reported in 99 species belonging to 59 genera and 24 families (Table 2) of the flora of south-west Western Australia. Because of its appearance in a wide taxonomic range, apparently with different mechanisms, the strategy has almost certainly arisen independently a number of times. Within one genus there can be both diallagous and non-diallagous taxa, e.g. *Verticordia*, *Petrophile*, *Leucopogon*. Passage into the diallagous state occurs gradually as summer progresses, presumably in response to dwindling soil moisture. Although my observations indicate that all or most plants of a species

behave similarly, they are not necessarily the same in their appearance, individuals commonly differing in colour. This agrees with Gaff's (1981) statement that 'the degree of water stress survived without injury varies appreciably from one species to the next even within one genus'. I suggest that soil moisture is critical, and variable, since a coloured plant may occur close to a green one.

In most species the rate of change to the coloured state and back to rehydration is much slower than in *Borya*, in which regreening takes 3-5 days (Gaff 1981). I suggest that the slower change in diallagous plants is due to the soil moisture level, which would decline more gradually in the deeper soils where most of the newly recorded species occur, compared to the shallow soils on granitic outcrops where *Borya* species grow. Most species listed here, especially the dicots, change gradually during the summer, only reaching maximum 'autumn colour' in February/March/April. Any effective rainfall will halt or reverse the change. I suggest that an effective fall is at least 5 mm, and more likely 10-15 mm, within a short period, e.g. 24 hours. In this recent season, a fall of ca. 12 mm (measured in a domestic gauge) in Kardinya (a suburb of Perth) was sufficient to start *Templetonia retusa* turning green, whereas less than 5 mm elsewhere in the Perth metropolitan area was insufficient. This is in line with observations in the Wiluna area, Western Australia, by Arnold (1963) and in southern Africa by Gaff (1977), who reported full rehydration after 10 mm. In contrast to the African plants that Gaff (1977) reported (from a winter-dry region), the Western Australian examples are from a summer-dry region and hence withstand both drought and high temperatures (commonly over 35 °C in the shade, and many of them receive no or little shade except just after sunrise and before sunset).

The diallagous condition is to be seen through much of the south-west, from the coast to the wheatbelt. In the recent record long, dry summer, 'autumn' colours were evident on Rottnest Island, at Naval Base, Seabird near Lancelin, the Darling Scarp, and in the kwongan around Badgingarra and Tammin. In previous years I have recorded it near Mt Lesueur, Chittering, Manmanning, Meenaar, Corrigin, Kulin and Little Darkin Swamp. In 2001, others reported it at Dragon Rocks Nature Reserve and Ravensthorpe (M Pieroni, M Bennett, personal communication).

Both fire-tolerant (seeder) and fire-sensitive (sprouter) species are diallagous. Most arborescent plants remain green during the summer, but some species of *Casuarina* change in certain locations, and *Acacia acuminata* has also been seen with yellowish-green phyllodes north of Moora and north of Badgingarra.

Nor is habitat a deciding factor. At any one site one can see both diallagous and non-diallagous plants. I have seen the condition on a number of soil types, from deep sand to clay and loam. The heavier soils do, however, seem to become drier as summer proceeds and there are usually fewer or no species in those soils that flower during autumn. The exception may be species of *Eucalyptus*. Plants in low-lying areas subject to winter damp or inundation can also show diallagy once the soil moisture diminishes, e.g. north and south of Badgingarra on the Brand Highway.

In some years, a prolonged dry season can lead to death rather than diallagy. This happened last summer, when the 2000 wet season ended suddenly at the end of September. Along the Darling Scarp, considerable deaths occurred in March and April, e.g. *Hemigenia*, *Eucalyptus wandoo*, *Dryandra sessilis*. Likewise along the scarp above the Swan River in Kings Park, there were deaths in *Dryandra sessilis* var *cygnorum* and *Dodonaea lackettiana*.

Generally I have recorded species that change colour. It may be assumed that others at the localities sampled retained a normal green appearance. But this work is very preliminary; far more is needed to confirm these data and discover the extent of the strategy.

Autumn flowering, budding and fruiting

Flowering

In contrast to the strategies described above, quite a few species have their normal flowering during late summer and autumn. The following summary includes many of these. It excludes many more that may commonly be seen with a few summer flowers, usually as a result of late spring or unusual summer rains. The structure, anatomy and physiology of one widespread summer flowerer, *Banksia prionotes*, has been studied by Pate *et al.* (1998). It has adapted to do so when soil moisture is at its lowest and temperatures can be very high. It follows that if there are flowers and developing fruits in summer and autumn then there is an associated fauna pollinating and predating them. Have these, or at least some, retained a summer/autumn flowering pattern from their tropical origin? They will certainly attract pollinators, given the much lower number of species in flower. Some have scented flowers.

Summary of taxa that flower in late summer and autumn

Some 29 taxa of *Banksia* (Proteaceae), of 67 in the south-west, flower during March/April and 13 of these begin to flower then (George 1984b, 1996).

Strangea cynanchicarpa (Meisn) F Muell (Proteaceae) flowers in February, but its south-western congener *S. stenocarpoides* flowers in spring.

Dryandra vestita Meisn (Proteaceae) is widespread in the northern kwongan and central wheatbelt and flowers in mid-summer. *Dryandra aurantia* A S George, a rare species from Little Darkin Swamp, flowers in mid to late autumn. In 1994, after a particularly dry summer, it was in full flower on 26 April.

In *Verticordia* (Myrtaceae), seven taxa typically flower in summer and autumn: *V. harveyi* Benth (January–April), *V. tumida* subsp. *therogana* A S George (November–March), *V. fastigiata* Turcz (February–July), *V. minutiflora* F Muell (January–June), *V. pityrhopis* A S George (February–June), *V. sieberi* Diesing ex Schauer (all varieties) (January–April), *V. vicinella* A S George (January–April). Thus, the one genus may contain both diallagous and summer/autumn-flowering species.

Four species of *Beaufortia* (Myrtaceae) are summer/autumn flowering: *B. sparsa* R Br, *B. anisandra* Schauer, *B. squarrosa* Schauer, *B. aestiva* K Brooks. Other such Myrtaceae are *Calytrix fraseri* A Cunn (typically in full flower during February and March), and *Scholtzia involucreata* (Endl) Druce (Myrtaceae).

More than 93 south-western taxa of *Eucalyptus* (Myrtaceae) flower regularly in the autumn, and of these some 30 begin to flower during this season (Brooker & Kleinig 1990). Taxonomically those taxa are spread throughout the genus and through many vegetation formations. They include both trees and mallees. Examples include *Eucalyptus calophylla*, *E. erythrocorys*, *E. wandoo*, *E. patens*, *E. gomphocephala*, *E. gardneri*, *E. salubris*, *E. eudesmioides*.

A curiosity in the flora is the parasitic *Pilostyles*, the only genus of the family Rafflesiaceae in Australia. The family is pan-tropical and temperate, and some species have spectacularly large flowers. *Pilostyles* occurs in South America and south-western Western Australia, a clear example of Gondwanan distribution. In the two Australian species, the flowers have become reduced to insignificant size (1.5–3 mm wide) but have retained a flowering time similar to that of their tropical relatives. Like *Nuytsia* and other mistletoes, they draw nutrients and water from their hosts, hence low soil moisture is less likely to affect them.

Several south-western mistletoes (Loranthaceae) are summer-flowering, e.g. *Amyema miquelii* (Miq) Tieghem, *A. preissii* (Miq) Tieghem. Summer-flowering species of *Acacia* (Mimosaceae) include *A. microbotrya* Benth and *A. huegelii* Benth. Autumn-flowering species of *Daviesia* (Papilionaceae) include *D. abnormis* F Muell, *D. angulata* Benth, *D. chapmanii* Crisp, *D. epiphyllum* Meisn and *D. speciosa* Crisp.

Pithocarpa (Asteraceae), a small genus of perennial daisies endemic in the south-west, flowers from late summer to autumn. It shows vegetative growth during winter and spring, is semi-deciduous, and then produces everlasting-type flower heads. Some species of *Olearia* (Asteraceae) are summer/autumn flowering. During field work for this paper in 2001, I recorded *O. paucidentata* (Steetz) Benth in full flower at Charles Gardner Flora Reserve, south of Tammin, on 10 March; interestingly it was still in flower on 7 June. *Olearia muricata* (Steetz) Benth was in late flower and fruit at Pinjarrega Nature Reserve, north-west of Watheroo, on 1 April.

The Sandalwood (*Santalum spicatum* (R Br) DC. (Santalaceae) flowers in summer. On 10 March 2001 it was in full flower at Charles Gardner Reserve. Several species of *Platysace* (Apiaceae) are summer-flowering, e.g. *P. cirrosa*, *P. juncea*, *P. effusa*, *P. sylvatica* and *P. peltigera*.

The yam *Dioscorea hastifolia* Endl (Dioscoreaceae), the only south-western representative of the family, flowers in autumn and early winter and appears independent of rain, drawing instead on reserves in its tuber. In 2001, it began flowering profusely on the Darling Scarp at Forrestfield in late April, before any rain fell.

The creeping, stilt-rooted triggerplant *Stylidium repens* R Br (Stylidiaceae) retains green leaves throughout the year. It has two flowering periods, in autumn and spring, but will respond to unseasonal rain as occurred in January 2000. Flowers develop within days. In 2001, at Piesse Brook, new stilt roots were also well developed 16 days after the first effective rain.

A number of species flower within days of the first effective rains, e.g. in Cyperaceae (*Lepidosperma*, *Schoenus*),

Restionaceae (13 species, Meney & Pate 1999), Epacridaceae (*Astroloma*, *Leucopogon*), Mimosaceae (*Acacia*).

Budding

Many native plants initiate buds soon after flowering in winter or spring and hold them at an early stage until shortly before flowering the following season. There are two general strategies, referred to by Bell & Stephens (1984) as 'long continuous' and 'long arrested' bud development. The latter is especially common among Epacridaceae, Fabaceae and Proteaceae and Restionaceae (Meney & Pate 1999), a number of species of which initiate buds soon after flowering, then become dormant during summer (e.g. *Dodonaea aptera*, *Leucopogon insularis*, *Astroloma serratifolium*, *Hovea pungens*, *Templetonia retusa*). They appear to remain 'viable' even if the plant is diallagous. Growth recommences with the first rains, and some flower very quickly, others during winter. 'Long continuous' bud development occurs over summer with no resting period. Noteworthy among these is *Stirlingia latifolia* (Blueboy) which develops its flowering stems during the late summer, autumn and winter before flowering in early spring. It is especially floriferous the first year after fire.

Fruiting

The Western Australian Christmas Tree (*Nuytsia*) not only flowers as the weather is coming to its hottest and driest but then continues throughout the summer to develop and ripen its fruit. And this not protected within the foliage or by large bracts or woody follicles, but exposed over the crown of the tree. Obviously, *Nuytsia* has an advantage over most other plants in drawing both nutrients and water from its hosts. The fruit of many woody-fruited Proteaceae are also growing and maturing during summer, e.g. *Hakea*, *Xylomelum*, as do many capsular-fruited Myrtaceae.

Conclusion

In this paper I have tried to reveal some little-known aspects of our flora and pointed the way to further study. There must be more fascinating dormancy mechanisms to be revealed, reasons to be discovered why some plants flower and fruit at such an inhospitable season, and why others require this kind of dormancy before they will flower properly, or even survive. Over the coming years I hope to see research into our autumn colours in particular, with, perhaps, some spinoffs into the agricultural and horticultural industries. Following are suggestions for research topics in diallagy.

- How extensive is the strategy taxonomically?
- How extensive is the strategy geographically? Can satellite imagery be used to map it?
- What is the internal mechanism? What happens to the anatomy? What is happening to the physiology?
- What are the root systems?
- Is there an association with a sudden increase in toxicity of some species of *Gastrolobium*?
- How long can plants remain in the diallagous state?
- How long do they take to regreen?
- Is there a benefit, if any, besides survival?

- Can this be used in genetic engineering, e.g. to transfer drought-tolerance to crop plants?

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References

- Arnold J M 1963 Climate of the Wiluna-Meekatharra area. CSIRO Australian Land Research Series 7:71-92.
- Bacci L, Devincenzi M, Rapi B, Arca B & Benincasa F 1998 Two methods for the analysis of colorimetric components applied to stress monitoring. Computers & Electronics in Agriculture 19:167-186.
- Beard J S 1968 Drought effects in the Gibson Desert. Journal of the Royal Society of Western Australia 51:39-50.
- Bell D T & Stephens L J 1984 Seasonality and phenology of kwongan species. In: Kwongan: Plant Life of the Sandplain (eds J S Pate & J S Beard). University of Western Australia Press, Nedlands, 205-226.
- Bowen G D 1981 Coping with low nutrients. In: The Biology of Australian Plants (eds J S Pate & A J McComb). University of Western Australia Press, Nedlands, 33-64.
- Brooker M I H & Kleinig D A 1990 Field Guide to Eucalypts. Inkata Press, Melbourne and Sydney.
- Churchill, D M 1985 Three new species of *Borya* Labill. (Liliaceae). Muelleria 6:1-8.
- Churchill, D M 1987 *Borya*. In Flora of Australia 45 (ed A S George). Australian Government Publishing Service, Canberra, 268-279.
- Connor D J & Doley D 1981 The water relations of heathlands: physiological adaptation to drought. In: Heathlands and Related Shrublands: Analytical Studies. Ecosystems of the World Vol 9B (ed R L Specht). Elsevier Scientific Publishing, Amsterdam, 131-141.
- Dawson T E & Pate J S 1996 Seasonal water uptake and movement in root systems of Australian phreatophytic plants of dimorphic root morphology - a stable isotope investigation. Oecologia 107:13-20.
- Gaff D F 1977 Desiccation tolerant vascular plants of Southern Africa. Oecologia 31:95-109.
- Gaff D 1981 The biology of resurrection plants. In: The Biology of Australian Plants (eds J S Pate & A J McComb). University of Western Australia Press, Nedlands 114-146.
- Gaff D & Latz P 1978 The occurrence of resurrection plants in the Australian flora. Australian Journal of Botany 26:485-492.
- George A S 1984a An Introduction to the Proteaceae of Western Australia. Kangaroo Press, Kenthurst.
- George A S 1984b, 3rd edn 1996 The Banksia Book. Kangaroo Press, Kenthurst.
- George A S 2002 The Long Dry: Bush Colours of Summer and Autumn in South-western Australia. Four Gables Press, Kardinya.
- George A S & Hnatiuk R J 1978 A vegetation and flora reconnaissance of Avon Location 19769. Western Australian Herbarium Research Notes 1:19-27.
- Hellmuth E O 1971 Eco-physiological studies on plants in arid and semi-arid regions in Western Australia III Comparative studies on photosynthesis, respiration and water relations of ten arid-zone and two semi-arid zone plants under winter

- and late summer climatic conditions. *Journal of Ecology* 59:225-260.
- Hnatiuk R J & Hopkins A J M 1980 Western Australian species-rich kwongan (sclerophyllous shrubland) affected by drought. *Australian Journal of Botany* 28:573-585.
- Lamont B B 1984 Specialised modes of nutrition. In: *Kwongan: Plant Life of the Sandplain* (eds J S Pate & J S Beard). University of Western Australia Press, Nedlands, 126-145.
- Main B Y 1967 *Between Wodgil and Tor*. The Jacaranda Press, Brisbane & Landfall Press, Perth.
- Meney K A & Pate J S 1999 *Australian Rushes: Biology, Identification and Conservation of Restionaceae and Allied Families*. University of Western Australia Press, Nedlands & Australian Biological Resources Study, Canberra.
- Meney K A, Dixon K W & Pate J S 1993 Occurrence of vesicular mycorrhizal fungi in dryland species of Restionaceae and Cyperaceae from south-west Western Australia. *Australian Journal of Botany* 41:733-737.
- Montague K D & Woo K C 1999 Recovery of tree photosynthetic capacity from seasonal drought in the wet-dry tropics: the role of phyllode and canopy processes in *Acacia auriculiformis*. *Australian Journal of Plant Physiology* 26:135-145.
- Paczkowska G & Chapman A R 2000 *The Western Australian Flora A Descriptive Catalogue*. Wildflower Society of Western Australia, Western Australian Herbarium CALM, & Botanic Gardens & Parks Authority, Perth.
- Pate J S & Dixon K W 1981 Plants with fleshy underground storage organs—a Western Australian survey. In: *The Biology of Australian Plants* (eds J S Pate & A J McComb). University of Western Australia Press, Nedlands, 181-215.
- Pate J S & Meney K A 1999 Morphological features of Restionaceae and allied families. In: *Australian Rushes: Biology, Identification and Conservation of Restionaceae and Allied Families* (eds K A Meney & J S Pate). University of Western Australia Press, Nedlands & Australian Biological Resources Study, Canberra, 3-23.
- Pate J S, Jeschke W D, Dawson T E, Raphael C, Hartung W & Bowen B J 1998 Growth and seasonal utilisation of water and nutrients by *Banksia prionotes*. *Australian Journal of Botany* 46:511-532.
- Pate J S, Weber G & Dixon K W 1984 Stilt plants—extraordinary growth form of the kwongan. In: *Kwongan: Plant Life of the Sandplain* (eds J S Pate & J S Beard). University of Western Australia Press, Nedlands, 101-125.
- Pook E W, Costin A B & Moore C W E 1966 Water stress in native vegetation during the drought of 1965. *Australian Journal of Botany* 14:257-267.
- Wilson K L 1997 New species of Cyperaceae in Western Australia. *Nuytsia* 11:269-282.